# Fossil crabs (Crustacea: Decapoda: Brachyura) from the latest Miocene Senhata Formation, Boso Peninsula, Japan

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Abstract. Two species of fossil decapods, *Maja tomidai* sp. nov. and *Daldorfia* sp. are described from the latest Miocene Senhata Formation of the Boso Peninsula, central Japan. The former species resembles *Maja morii* Kato from the middle Miocene of Japan and *Maja dominoleuae* Hu and Tao from the late Miocene of Taiwan. A large palm of *Daldorfia* sp. is the third fossil record of the genus from Japan. The discovery of *Daldorfia* sp. supports the existence of subtropical to tropical marine conditions in the latest Miocene of the Boso Peninsula indicated previously by molluscan evidence.

Key words: Brachyura, Crustacea, Daldorfia, Decapoda, Maja, Senhata Formation, Zushi Fauna

## Introduction

Decapod Crustacea from the upper Miocene of Japan have previously been reported from the Tano and Aya formations of the Miyazaki Group, Kyushu (4 species; Karasawa, 1993, 1997; Karasawa and Kato, 1996); the Uchiumigawa Group, Kyushu (1 species; Karasawa, 1990); the Itahana Formation of the Tomioka Group, central Japan (8 species: Kato, 2001); the Aoso Formation, north of Sendai (1 species; Karasawa and Kato, 1996), and the Wakkanai Formation, Hokkaido (1 species; Imaizumi, 1952).

Two species of decapod crustaceans were obtained from exposures of the upper Miocene Senhata Formation in the Matsukura Kogyo Quarry in Motona, Kyonan Town, Chiba Prefecture  $(35^\circ 9' \text{ N}, 135^\circ 51' \text{ E})$  (Figure 1). A specimen found by S. Tomida represents a new species of the majid genus *Maja*. Several additional fragmentary specimens were subsequently collected from the same locality by N. Kaneko and donated to the Natural History Museum and Institute, Chiba. The other specimen collected by K. Usui is identified as a large palm belonging to the daldorfiid genus *Daldorfia*.

The purpose of this paper is to describe the new species of *Maja* and the undetermined species of *Daldorfia*, and to discuss their phylogenetic and paleobiogeographic implications. The material described herein is deposited in the Mizunami Fossil Museum (MFM) and Natural History Museum and Institute, Chiba (CBM-PI).

#### Locality and paleoenvironments

The Senhata Formation exposed at the present locality is up to 130 m in thickness and is composed mainly of coarsegrained sediments, intercalating mudstones and pyroclastics (Yabe and Hirayama, 1998). The formation yields abundant remains of marine animals such as molluscs, hermatypic corals, bryozoans, isopods, echinoids, elasmobranchs and mammals.

The geologic age of the Senhata Formation has been discussed from various viewpoints. Ibaraki and Tsuchi (1980) assigned the formation to Blow's (1969) planktonic foraminifera Zone N17. Kanie *et al.* (1991) reported calcareous nannofossils indicative of the CN9 Zone of Okada and Bukry (1980) from the underlying Amatsu Formation and the CN10b Zone from the overlying Inakozawa Formation. Kasuya (1987) reported a fission-track age of  $6.3 \pm 0.4$  Ma for the Ok tuff bed in the lower part of the Inakozawa Formation. To sum up these data, the geologic age of the Senhata Formation is regarded as the latest Miocene.

O'Hara and Ito (1980) studied the molluscs of the Senhata Formation and noted that the assemblage is a mixture of relatively worn and fragmented shells of shallowwater inhabitants and well preserved shells of deep-water dwellers. They concluded that the shallow-water



Figure 1. Map showing the fossil locality.

assemblage was mixed with a bathyal assemblage as a result of short distance transportation by bottom currents. Tomida (1989, 1996) recognized seven types of molluscan assemblages in the formation. He also considered the molluscan assemblage of the present locality to be a mixture of both a bathyal assemblage (200–250 m in depth on the continental slope) and mesoneritic to subneritic assemblages that were transported from shallower waters. Based on the occurrences of the isopod *Palaega*, Karasawa *et al.* (1992) suggested an upper bathyal paleoenvironment for the Senhata Formation.

Tomida and Itoigawa (1986) and Tomida (1989) reported the occurrences of the planktonic gastropod *Hartungia* sp. and cephalopods such as *Aturia* and *Argonauta* in various growth stages from the present locality. Based on the presence of these characteristic genera and other subtropical to tropical molluscs, Tomida (1983, 1996), Tomida and Itoigawa (1986) and Ozawa and Tomida (1992, 1996) deduced that the Senhata Formation was deposited under the influence of warm-water currents. In their study of the selachian (shark) assemblage of the Senhata Formation, Yabe and Hirayama (1998) also concluded that this formation was deposited in the upper part of the continental slope under the influence of warm-water currents.

Ozawa and Tomida (1992) and Ozawa *et al.* (1995) proposed the term "Zushi Fauna" for some late Miocene to early Pliocene molluscan assemblages on the Pacific side of Japan which contain molluscan species indicative of tropi-



Figure 2. Localities of fossil *Daldorfia* species. Distribution of the Zushi Fauna and reconstruction of paleogeography are modified after Ozawa and Tomida (1992), Ogasawara (1994) and Nakamura *et al.* (1999). The paleoclimatology is based on Ogasawara's (1994) divisions.

cal to subtropical marine climates (Figure 2). They correlated this warmer marine climate with "Climatic Optimum 3" of Barron and Baldauf (1990).

Among the decapod genera here described, the genus Maja has 16 living species, of which 13 occur in the Indo-West Pacific (Griffin and Tranter, 1986) and 7 in Japanese warm-temperate to tropical waters south of the Boso Peninsula, central Japan (Sakai, 1976). The genus Daldorfia includes 6 living species in tropical to subtropical Japanese waters (Sakai, 1976). Particularly, D. horrida (Linnaeus, 1758), the most closely related to D. sp. from the Senhata Formation, inhabits tropical to subtropical waters south of the Kii Peninsula in Japan, the area washed by the warm Kuroshio Current (Sakai, 1976). Judging from the distributions of living species, the decapod species found in the Senhata Formation support the view previously suggested by molluscan evidence that a warm marine climate existed along the Pacific coast of Japan in the latest Miocene.

Fossil species of *Daldorfia* have hitherto been recorded from the upper Miocene of Japan and Oligocene of North America. They are *D. nagashimai* Karasawa and Kato, 1996 from the Aya Formation, Miyazaki Group in southwest Japan, *Daldorfia* sp. from the Aoso Formation in northeast Japan (Karasawa and Kato, 1996; Figure 2), and *Daldorfia himaleorhaphis* Schweitzer, 2001a from the Jansen Creek Member of the Makah Formation in the Olympic Peninsula, Washington State, the United States of America.

The Aya Formation yields molluscan species typical of the "Zushi Fauna" (Nakamura et al., 1999). While Ozawa and Tomida (1992) suggested that the "Zushi Fauna" extended north into the Fukuda Formation, south of Sendai, the occurrence of Daldorfia sp. from the Aoso Formation indicates that the fauna extended north of Sendai, where a warm-water event is suggested by molluscs (Ogasawara, 1994) and planktonic foraminiferal assemblages correlative with "Climatic Optimum 3" of Barron and Baldauf (1990) (Saito and Isawa, 1995). The occurrences of Daldorfia spp. from the Aya, Senhata and Aoso formations provide additional biotic evidence for the warming event in the late Miocene to early Pliocene in northeast Japan. The occurrence of the oldest known species of Daldorfia, D. himaleorhaphis from the Oligocene of Washington State, is considerably distant geographically from the distribution of living species of this genus. However, the high diversity of the decapod assemblages, including subtropical species from the Eocene to Oligocene of the Pacific North America, indicates a much warmer marine climate in this area than prevails today (Schweitzer, 2001b).

#### Systematic descriptions

Section Heterotremata Guinot, 1977 Superfamily Majoidea Samouelle, 1819 Family Majidae Samouelle, 1819 Subfamily Majinae Samouelle, 1819 Genus *Maja* Lamarck, 1801

*Type species.—Cancer squinado* Herbst, 1788. By subsequent designation (ICZN opinion 511).

Discussion. — Based upon larval morphology, Rice (1983) proposed a phylogenetic relationship between genera within the family Majidae, regarding Maja as a "primitive" and Leptomithrax as an "advanced" form. Several previous studies also supposed the same relationship between the two genera (e.g. Kurata, 1969). The cup-shaped orbit of living species of Leptomithrax (three closely spaced orbital spines and the antennal fossa excluded from the orbit) is generally regarded as more "complete" than that of Maja (separate spines with an antenna included within the orbit). However, the orbital features of the early middle Miocene Maja morii Kato, 1996 from Japan resemble those of Leptomithrax, including its postorbital spine which exhibits an excavated anterior surface like that

typically observed in Leptomithrax (Griffin, 1966).

With respect to the posterior end of the carapace, the Japanese fossil *Maja* species, *M. morii* and the new species discussed herein have a single tubercle on the posterior end of the carapace as in *Leptomithrax longipes* (Thomson, 1902), a living species found in Australia and New Zealand. In its adult and larval morphologies, *L. longipes* was regarded as unique among the members of the genus *Leptomithrax* (Webber and Wear, 1981; McLay *et al.*, 1995).

Judging from these characters the phylogenetic relationship between *Leptomithrax* and *Maja* should be reconsidered. The oldest fossil record of *Maja* is from the early Miocene (*Maja robinsoni* Jenkins, 1985 from South Australia), while that of *Leptomithrax* extends into the late Eocene (*Leptomithrax griffini* Feldmann and Maxwell, 1990 from New Zealand), suggesting that *Maja* is a more advanced form than *Leptomithrax*.

Geologic range.-Miocene to Recent.

#### Maja tomidai sp. nov.

#### Figures 3.1a-c, 4, 5B

*Diagnosis.—Maja* with moderately long, divergent rostrum; lateral and dorsal spines acute. Intercalated and postorbital spines approximated. Dorsal regions densely covered with large, conical tubercles. Posterior end of carapace bearing single conical tubercle.

Description.-Carapace pyriform in outline. Rostrum bifid, acute, widely divergent anterolaterally. Orbit rounded. Supraorbital eave thick, sparsely granulate. Antorbital spine acutely triangular, directed laterally, slightly curved posteriorly. Intercalated spine short, triangular, about half length of antorbital and one-third length of postorbital spines. Postorbital spine triangular, directed anteriorly. Intercalated and postorbital spines closely approximated. Basal antennal article directed forward with anteromedial and anterolateral spines. Anterolateral margin of carapace bears acute, long hepatic spine and three acute branchial spines; posteriormost one lies dorsally. Dorsal regions well defined. Gastric, branchial, and hepatic regions strongly convex, covered with pointed, variable-sized conical tubercles. Frontal region with two longitudinal series of conical tubercles; tubercles extending to base of rostrum, increasing in size posteriorly. Mesogastric region strongly convex with two large, conical tubercles arranged longitudinally. Metagastric region also highly convex with large median tubercle. Urogastric region with conical tubercle markedly smaller than others. Cardiac region strongly convex, defined laterally by broad, plain furrows, and medially by a large, conical tubercle. Intestinal region elevated, forming acute spine. Hepatic region with clustered tubercles, bordered by broad, plain depressions. Branchial re-



Figure 3. 1. Maja tomidai sp. nov., MFM 83053. Holotype. a and b, outer and medial surface of the right chela,  $\times 1.5$ ; c, carapace,  $\times 1.0$ . 2. Daldorfia sp., CBM-PI 01084, manus of right chela; a ; outer surface, b ; medial surface. CBM-PI 01084,  $\times 0.5$ . Scale bars = 10 mm.

gions with numerous variable-sized tubercles. Sinuous swellings extending parallel to branchiocardiac groove consisting of large tubercles. Metabranchial region convex with sparse tubercles and granules, less developed than mesobranchial and intestinal swellings. Posterolateral margin rimmed, sinuously convex. Posterior end of carapace bearing one large, conical, axial tubercle. Palm of right cheliped slightly curved upward; preserved part of outer surface smooth. Fingers acute, slender, obviously curved downward.

Discussion.—In carapace outline, the present species most resembles *Maja dominoleuae* Hu and Tao, 1985 from the upper Miocene of Taiwan. However, *M. tomidai* sp. nov. is easily distinguished from *M. dominoleuae* in that the orbital spines are shorter and slightly curved upward, and the dorsal surface of the carapace is densely covered by



Figure 4. Line drawing showing the dorsal view of carapace of *Maja tomidai* sp. nov. The specimen is compressed obliquely, causing the right half of the carapace to be displaced anteriorly. Scale bar = 10 mm.

large tubercles. *Maja tomidai* sp. nov. resembles *M. morii* Kato. 1996 from the early middle Miocene of the Chichibumachi and Takaku groups, Saitama and Fukushima prefectures, Japan (Kato and Karasawa, 1995) in the general arrangement of tubercles and lateral spines of the carapace, but differs in having denser tubercles and more elongated spines on the dorsal surface. In addition, the antennal fossa of *Maja morii* seems to lie outside the orbit, while that of *Maja tomidai* is included within the orbit like living species of *Maja* (Figure 5).

Despite these differences, *M. tomidai* sp. nov. shares the following important characters with *M. morii*: (1) the three orbital spines are relatively approximated, and (2) the posterior end of the carapace has a single conical tubercle. Most living species of *Maja* possess a pair of spines or tubercles on the posterior end of the carapace, and no species in this genus has a large, single tubercle on the posterior end of the carapace like *M. tomidai* sp. nov. and *M. morii*. Due to the incompleteness of known specimens, unfortunately, the ventral orbital features and the posterior end of the carapace of *M. dominoleuae* are not available.

The carapace of the holotype is compressed and severely deformed (Figure 4).

Material examined.—MFM 83053 (Holotype: carapace and appendages). CBM-Pl 01085-01087.

*Etymology.*—Named after Susumu Tomida who contributed greatly to the paleontology of the Senhata Formation and discovered the holotype specimen.

Measurements.-Holotype, maximum carapace length



Figure 5. Line drawing showing the ventral orbital features of (A) Maja morii Kato, 1996 (CBM-PI 00177, Numanouchi Formation, Takaku Group) and (B) Maja tomidai sp. nov. (holotype). Abbreviations: Ot, orbit, Rt, rostrum, af, antennal fossa, ba, basal antennal article, ps, postorbital spine, se, supraorbital eave. Scale bar = 10 mm.

(including rostrum), 78.0 mm; maximum carapace width (excluding the branchial spines), 43.5 mm. Palm length, 37.0 mm.

# Superfamily Parthenopoidea MacLeay, 1838 Family Daldorfiidae Ng and Rodriguez, 1986 Genus *Daldorfia* Rathbun, 1904

*Type species.*—*Cancer horridus* Linnaeus, 1758. By monotypy.

Geologic range.-Oligocene to Recent.

#### Daldorfia sp.

### Figure 3.2a, b

Description.—Manus of right cheliped without fixed finger large (length, 131 mm), strongly compressed; upper and lower margins diverging distally. Lateral and medial surfaces densely nodose. Nodes conical to irregular; variable in size up to 20 mm in diameter; surface bearing clusters of various-sized tubercles. Furrows between nodes shallow, smooth except for scattered small conical tubercles. Superior socket of articulation, situated near dorsoproximal corner of manus and directed proximally. Proximal margins of lateral and medial surfaces bearing rounded, thick rims along articulation with carpus.

Discussion.—The previously known fossil record of this genus from Japan includes Daldorfia nagashimai Karasawa and Kato, 1996 from the latest Miocene Aya Formation, Miyazaki Group in southwest Japan and D. sp. from the late Miocene Aoso Formation to the north of Sendai in northeast Japan (Karasawa and Kato, 1996) (Figure 2). Daldorfia? sp. from the middle Miocene Aoki Formation in central Japan (Karasawa et al., 1999) is too incomplete to permit generic assignment. It may belong to a species of the Majidae. Therefore, Daldorfia sp. described here is the third fossil record for this genus from Japan.

Living species of *Daldorfia* are inhabitants of littoral and sublittoral zones (Sakai, 1976). Judging from the disarticulated and incomplete state of the present specimen, it may have been transported from a littoral or sublittoral zone, together with shallow-water molluscs, to the deeperwater environment of the Senhata Formation.

Material examined.—CBM-PI 01084.

Measurements.—Manus length, 131 mm, manus height, 88 mm.

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